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STUDIES FOR STUDENTS.

GEOLOGIC STUDY OF MIGRATION OF MARINE INVERTEBRATES.

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INTRODUCTION.

THE migration of invertebrates is necessarily too slow to be observed in a few years, and only many successive generations of observers could throw light on it. While the present habits of these animals may be studied and inferences drawn as to their history, these inferences are probably often incorrect. The common inference that fossil corals indicate a warm sea is an example; by this method the existence of a tropical sea in the Arctic regions during Palæozoic time has been inferred, and therefore great changes in physical geography. But it is well known that the elephant and the rhinoceros, which we regard as typical tropical animals, lived in the Arctic regions of the northern hemisphere during the Glacial period. Also the Bryozoan group Cyclostomata are, as fossils, widely distributed in temperate regions, but the living forms of these are decidedly Arctic.

The present distribution of animals shows many anomalies, many groups being present where naturally, according to their habits elsewhere, they ought to be lacking, and being absent where, according to analogy, they ought to be present.

It is clear then that a study of the present distribution and habits of marine animals can throw little light on their history. But the geologist does not confine his observations to the present; geologic history is a book whose leaves are scattered in many parts of the earth, and each observer gathers some of these leaves.

A study of the distribution of animals in past time ought to explain their present occurrence, and the laws governing their distribution; and incidentally light should be thrown on the extinction of faunas, and upon changes in physical geography that accompanied and caused the migrations and extinctions.

ZOÖLOGICAL PROVINCES.

Modern Provinces.—One of the first facts in the study of geographic zoölogy that attracted the attention of naturalists was that animals are not distributed strictly according to climate, or other physical conditions. This was inexplicable, according to the views then held. The work of Edward Forbes upon the *Natural History of the European Seas* began the scientific study of the distribution of marine animals. Forbes formulated the theory of generic and specific centers. Each genus and each species was to him a reality, and by distribution of these from the centers he satisfactorily accounted for their occurrence in other places. Although reasoning upon the theory of special creation for each species, Forbes recognized the fact that species and genera are never intermittent except locally. His results therefore do not differ in any respect from those obtained on the basis of development of one species out of another. He showed too that while separated regions under the same conditions show great similarity of faunas, this similarity is due rather to representative than to identical species or genera. What better argument could be adduced for the influence of surroundings on development?

S. P. Woodward[1] while working upon the same theory as Forbes reaches the following conclusion: "Meanwhile it may be stated that according to this evidence [that derived by Forbes from Palæontology] the faunas of the provinces are of various ages, and that their origin is connected with former (often very remote) geological changes, and a different distribution of land and water over the surface of the globe." It must be remembered that this was written several years before the publication of Darwin's *Origin of Species*, at a time when the teachings of Lamarck had been practically forgotten, and by an author that believed in the reality of species.

The marine provinces that were proposed by Woodward[2] for the invertebrates hold good even now. They are as follows: (1) Arctic, (2) Boreal, (3) Celtic, (4) Lusitanian, (5) Aralo-Caspian, (6) W. African, (7) S. African, (8) Indo-Pacific, (9) Australo-Zealandic, (10) Japonic, (11) Aleutian, (12) Californian, (13) Panamic, (14) Peruvian, (15) Magellanic, (16) Patagonian, (17) Caribbean.

And these provinces[3] are grouped naturally into great regions:

"The tropical and sub-tropical provinces might naturally be grouped in three principal vivisions, viz., the Atlantic, the Indo-Pacific, and the West-American,—divisions which are bounded by meridians of longitude, not by parallels of latitude. The Arctic province is comparatively small and exceptional; and the three most southern faunas of America, Africa, and Australia differ extremely, but not on account of climate." An application of this same method enabled Wallace to write his *Geographical Distribution of Animals* and to place the study of the geographic distribution of all animals on a scientific basis.

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[1] Manual of the Mollusca, 1856, p. 352.

[2] Manual of the Mollusca, 1856.

[3] Loc. cit., p. 353.

ANCIENT PROVINCES.

There were no such things as universal faunas, even in remote geologic time; there have always been barriers of continent and ocean, and probably too of climate, ever since life existed on the earth. Only the deep sea faunas could be universal, if oceanic bottoms had been stable, but even they are not universal now, nor have they remained unchanged in time.

Barrande showed that the known Cambrian and Silurian faunas could be divided into well-defined provinces, and the recent work of Professor Walcott has extended greatly our knowledge of the distribution of Cambrian animals.

For the geographic study of Devonian faunas we are especially indebted to Barrende,[1] and H. S. Williams.[2]

It has been shown conclusively by the latter author that in Lower and Middle Devonian there was a North-South American region, and a Eurasian region; and that during Upper Devonian times the regions had changed so that the grouping was into the Eurasian-North American, and the South American-South African.

We owe most of our knowledge of the faunal geography of the Carboniferous to Professor Waagen.[3] He has shown that during the Carboniferous there were two great regions corresponding to the northern and the southern hemispheres, and that within these were provinces more or less sharply defined. But these regions and provinces by no means agreed with those of the older Palæozoic.

Mojsisovics[4] has divided the known Triassic faunas into two great regions, the European and the Pacific, and these in turn into provinces; the European Mediterranean province, the Arctic; the Himalayan, which is intermediate between Arctic and Mediterranean; and the American.

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[1] Système Silur. Bohème.

[2] Cuboides Zone and its Fauna, Bull. Geol. Soc. Amer., Vol. I.

[3] Pal. Indica. Salt Range Fossils. Geological Results.

[4] Arktische Triasfaunen, Mém. Acad. Sci. St. Petersbourg, VII. Series, Vol. XXXIII., No. 6.

But during the Lower Trias the Arctic, the Himalayan, and the American provinces had closely allied faunas, and might be grouped together in contrast to the Mediterranean. In the Middle Trias, however, the American Triassic province was being gradually cut off from the Arctic, and communication established with the Mediterranean. This connection through the Himalayan province was very complete in the Upper Trias, and all three might be grouped under one region, the Mediterranean-Indian-American.

Neumayr[1] has worked out the provinces of Jurassic time, and grouped them in two regions, the Boreal, and the Central-Mediterranean. He has also traced out for that time the distribution of climatic zones by means of the Boreal type, the North Temperate type, the Alpine or Equatorial, and the South Temperate.

To the Boreal region belong the Russian, the Siberian, the Himalayan, and the Alaskan provinces. To the Central Mediterranean region belong the Northern European, the Alpine, the Salt Range, the Southern Indian, the Australasian, South American, and the Western American. But during Upper Jura the Western American province took on an Arctic character, and certainly became part of the Boreal region. Thus these regions and provinces will not hold good for any long-time division, but were always, though slowly, changing.

The study of the distribution of fossil faunas as influenced by climate was begun by Ferdinand Roemer,[2] who recognized that the Cretaceous of England, northern France and Germany has a fauna similar to that of New Jersey, and that the faunas of southern Europe, north Africa, and Texas are similar. These differences Roemer ascribed to climate, noting that at that time, as today, in America the isothermal lines came much further south han in Europe. Neumayr[3] has carried these studies forward, correlating the various observations made since Roemer's time

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[1] "Geogr. Verbreitung der Juraformation," and "Klimatische Zonen wärend Jura und Kreidezeit."

[2] Kreidebildungen von Texas, Bonn, 1852.

[3] Klimatische Zonen wärend Jura und Kreidezeit.

It is now known that the Cretaceous of South America belongs to the tropical type, as does also that of Mexico.

Still more recent observations have shown that the Cretaceous of western North America belonged during the Neocomian or Knoxville to the Boreal or Russian type, but this resemblance soon died out, and that the Horsetown or Gault fauna was of central European type, like that of India. This kinship to the Indian faunas persisted until the end of the Cretaceous. Since Cretaceous time the marine provinces seem to coincide closely with the existing boundaries of the temperature and shore lines.

MIGRATION.

Causes of migration.—The lower forms of life produce many more young than can possibly come to maturity; hence a lively competition ensues between those of like character as well as between those that are different. Under these conditions an equilibrium is attained, the field supports the maximum population, and all others migrate or perish.

Thus migration would be a necessity even if the conditions remained always the same and the competition were always between members of the same fauna. But conditions never remain the same. The same causes drive individuals from one habitat and to another, and disturb the equilibrium there established. A disturbance taking place in an unimportant part of a province must therefore disturb the whole zoölogical region. And if we add to this changes in physical geography, we see that constant migration and intermigration must be a necessity. Any rising or sinking of shore lines would drive the inhabitants from their dwelling places; each change in the outline of continents changes the direction of currents, and thus has a marked influence on migration.

Extinction of faunas.—Today it is noticed that when the struggle for existence becomes too severe for a species it disappears. But the reason for this disappearance has always been uncertain. In geologic history a species has a certain length of life and dies out, never to reappear. The supposed contemporaneous extinction of a species all over the earth has led to the theory that species, like individuals, have a limited life, and that in time they reach a stage of development where they can go no further, and then of necessity die out.

This idea would be all very well if species dropped out one at a time, but in reality they usually go and come by faunas. It would seem, then, that changes in physical geography have had more to do with the extinction of faunas then anything else. This becomes the more probable when we reflect that species are not extinguished contemporaneously over the earth, but rather that their appearance and extinction have been used by geologists in a misleading way to prove synchronism of strata.

Remarkable cases of survival of types have long been known, as of *Trigonia* in the Australian waters, and of *Pholadomya* in the Antilles. Survivals of faunas are constantly coming to light. Dr. W. H. Dall[1] has shown that a large proportion of the Pliocene and even Miocene invertebrates of the Southern Atlantic Gulf states are still found living in the archibenthal region off the present coast. The same thing is true of the California coast, but here we have an even more remarkable example. Dr. A. C. Lawson,[2] from purely geologic evidence, has reached the conclusion that Santa Catalina Island has remained above water during Quaternary time, while most of the neighboring country was submerged. This stability of conditions has shown itself in a unique survival of the marine fauna, for Dr. Cooper's[3] list of the fossil mollusca of the California coast shows five species still living on Catalina that are known elsewhere only as fossils, and many species that are now known living in other remote zoölogical provinces. Similar cases of survival occur in ancient geologic formations.

Dr. C. R. Keys[4] called attention to a reappearance of a Waverly fauna in the Burlington of Missouri. A similar occurrence was described by the writer[1] and by Professor H. S. Williams[2] in the Fayetteville Shale, Lower Carboniferous, of Arkansas. A survival of a Devonian fauna in rocks of Lower Carboniferous age has been described from Nevada by Professor C. D. Walcott,[3] and from California by the writer.[4]

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[1] Bull. Mus. Comp. Zoöl., Vol. XII., No. 6, p. 186.

[2] Univ. Calif. Bull. Dept. Geol., Vol. I., No. 4, p. 135.

[3] Calif. State Mining Bureau, Seventh An. Rep. 1887.

[4] Am. Jour. Sci., Dec. 1892, p. 447.

It is becoming more evident all the time that the range of faunas, instead of being usually the same in widely separated regions, is usually different, and that strata can no longer be called synchronous from the occurrence in them of similar faunas.

In reality they can no longer be called homotaxial with any degree of certainty, unless we know in what direction the faunas migrated, since homotaxis in the palæontologic sense does not agree with homotaxis in the stratigraphic sense.

The extensive extinction of life at one place earlier than in another has also been noted. Professor W. Waagen[5] has suggested that the glaciation in the southern hemisphere toward the end of the Carboniferous killed off the Palæozoic flora earlier than was the case in regions where there was no glaciation. Such phenomena approach the nature of "catastrophes," and show that Cuvier's doctrine was not so far wrong after all.

The study of the distribution of faunas in the past seems to show that their extinction has been chiefly due to changes in physical geography; and that where conditions remained constant the faunas remained unchanged. This study too suggests that no part of the earth has remained unchanged, for while some of the abysmal regions may be very old, even their faunas are of comparatively modern aspect.

MEANS OF MIGRATION.[6]

Few invertebrates are rapid swimmers. Many are attached forms and the majority are only crawlers. But all are free at some time in the life of the individual or cycle. This is often in the larval state, but it is known that certain species of brachiopods, which are swimmers only in the *cephalula* stage, are distributed over thousands of miles. It is an important fact that ammonites, which were free in the adult stage, and may have been swimmers, though most probably chiefly crawlers, are not distributed much more widely than lamellibranchs or others of the lower invertebrates. Thus the Upper Triassic fauna of California contains many species that are found in the Alps and the Himalayas, and among these there are several species of the *Aviculidæ*, which in the adult stage were attached by a byssus. The Lower Cretaceous Knoxville fauna of California contains along with ammonites a good representation of European lamellibranchs; and the Horsetown and Chico faunas of California contain fully as many species of lower invertebrates as of ammonites that may with probability be referred to foreign species. It is clear, then, that their distribution has been due to faunal, rather than to individual migration. Faunal migration can only be possible under physical agencies acting slowly, and on a large scale. Marine currents along shore lines have been efficient aids to migration, not so much by transporting the young, as by transporting conditions suitable for life.

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[1] JOUR. GEOL., Vol. II., p. 198.

[2] Am. Jour. Sci., III. Ser. Vol. 49, pp. 94–101.

[3] Monograph VIII. U. S. Geol. Survey.

[4] JOUR. GEOL., Vol. II., p. 595.

[5] Pal. Indica. Salt Range Fossils. Geol. Results, p. 240.

[6] Accidental distribution need not be considered here; it may have occurred, but must have been very rare.

Even with our currents continental margins offer ample opportunities for faunal migration, for the crawling adults or the swimming young can find the constant conditions of depth, temperature and food supply suitable for their life.

Dr. W. H. Dall[1] has recently shown that tides on the archibenthal continental margins have been influential in distributing faunas. But probably the great agent of distribution has been the slow shifting of shore lines, which not only aids but also compels migration.

BARRIERS TO MIGRATION.

Land barriers.—Land masses present an insuperable barrier to all marine invertebrates; but if the bodies of land are short, and do not reach into polar waters, animals can easily pass around the ends. Thus the molluscan fauna of the Mediterranean does not differ appreciably from that of the English waters, because in the passage around the peninsula of Spain animals remain in temperate waters, and under nearly the same conditions.

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[1] Bull. Mus. Comp. Zoöl., Vol. XII., No. 6, p. 179.

On the other hand, the Isthmus of Panama separates two faunas absolutely distinct from each other; the same thing is true of the Isthmus of Suez.

East and west land masses would therefore not be very effectual barriers since they would not be so likely to extend into polar waters or into great differences of temperature.

Climatic zones.—That climatic zones are today partial barriers to migrants along the coast is shown by the difference in faunas living in northern and in southern latitudes under the same conditions. From the very nature of the case we should expect that cold water species would be able to cross climatic zones more easily than those adapted to warm water, since, as Dr. W. H. Dall[1] has shown, a fall of a very few degrees below the temperature favorable to life is more destructive than a rise of many degrees.

In the present we have no means of testing this, but facts brought to light by geology confirm it. The Jura of Central Europe and of the Argentine Republic in South America have the same fauna, which, in reaching one of these regions from the other, must have passed from temperate waters through tropical, and into temperate seas again. Also the faunas of the uppermost Jura and the lowest Cretaceous of Russia, which must have been Arctic in character, have migrated southward along the West Coast, almost into tropical waters. On the other hand we know of no case where equatorial faunas have passed through Arctic regions and even passages from tropical into temperate regions must be exceedingly difficult.

The genera *Lytoceras* and *Phylloceras* are common in the Neocomian, Lower Cretaceous beds of southern Europe; but although these waters were undoubtedly in direct connection with those of northern Europe, *Lytoceras* and *Phylloceras* are lacking in the latter region. Also in the lower part of the California Knoxville beds the above mentioned genera are unknown, and come in only higher up where the first members of the tropical Indian fauna began to come in.

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[1] Bull. Mus. Comp. Zoöl., Vol. XII., No. 6, p. 180.

Water barriers.—By far the greater part of marine animals live near the shore, and are unable to exist under other conditions. To these an abysmal sea is as impassible a barrier as a continent. But an east-west sea affords good opportunity for passage from one side to the other simply by slow progress along the margin. The fauna of the Mediterranean is a good evidence of this, the animals on the European shores not differing appreciably from those on the African.

And even on the opposite sides of great north and south oceans there are usually many species in common ; the Atlantic shore American fauna has many European species, and the Pacific shore harbors many from Asiatic waters. Their passage was effected in most cases along continental borders that have since been obliterated by subsidence and erosion. We have an abundance of independent geologic evidence that such recent changes have taken place, for example the destruction of the Antillean continent since Tertiary time, as worked out by Dr. J. W. Spencer.[1]

No doubt just such great recent changes in the distribution of land and water could be worked out in the Indian ocean, by application of the same method of study. The studies of Neumayr,[2] Waagen[3] and Suess[4] have demonstrated the existence of a continent in that region during late Palæozoic and early Mesozoic times, connecting Australia with Asia.

By a study of the geographic distribution of animals Wallace[5] has shown that in comparatively recent times Australia was

[1] Bull. Geol. Soc. Am., Vol. VI., 103–140.

[2] Geographische Verbreitung der Jura formation.

[3] Palæontologia Indica.

[4] Antlitz der Erde.

[5] Geograph. Distrib. Animals, Vol. II., The Australian region, pp. 387–485.

connected with many of the now scattered islands of the Indian Archipelago, but was separated from Asia.

Deep seas afford no barriers to rapid swimmers or to any pelagic forms, or to dwellers in the deeps. These approach much more nearly universal distribution, the first two being checked only by continental barriers, and the latter only by shallow waters.

CRITERIA OF MIGRATIONS.

Occurrence of identical or very closely related species and faunas in widely separated localities is good evidence of migration from one of these localities to the other, or from another region to both of them. In most cases, however, what are called identical species are in reality only representative forms.

As long as ideas about stratigraphic units were loose, and species had too broad a significance, it was impossible to recognize slight changes in faunas and age. Oppel[1] from his study of the Jura gave to geology the idea of stratigraphic zones, each with its characteristic animals. He recognized the importance of selecting types of great horizontal and narrow vertical distribution, and for this reason, where it was possible, chose ammonites as zone fossils.

This work would never have been possible had not Barrande[2] introduced an extremely narrow idea of species. Neumayr carried this study further by introducing the idea of "mutations" for genetic series of forms occurring in succeeding zones.

The use of these principles enables the naturalist to draw sharp lines between successive faunas.

Sporadic occurrence.—It is often noticed that species or faunas are intermittent in their occurrence, and this too when it is not due to difference of facies. Just such a case is the reappearance of the Waverly fauna in higher beds of the Lower Carboniferous of Missouri and Arkansas, already alluded to in this paper. The intercalations of marine beds in the fresh-water deposits of the Coal Measures is another good example.

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[1] Juraformation.

[2] Système Silur. Centre Bohème.

In the Jura of northern Europe, according to Neumayr,[1] the genera *Lytoceras* and *Phylloceras* appear only sporadically, being lacking entirely in sixteen zones; and the known species in that region do not belong to a genetic series. But in southern Europe these genera appear plentifully in all the zones, and do represent genetic series.

The migration northward at several successive periods is thus clearly established. In these same beds the genus *Amaltheus* also appears intermittently; but no region is yet known where *Amaltheus* developed continuously. Among the Jurassic ammonites of northern Europe there are a number of cryptogenic types, most of which coincide with the *Amaltheidæ* in their appearance and therefore came from the same region.

These facts go to show that the principles on which Barrande's[2] doctrine of colonies was founded were not far wrong, although it has since been found that his colonies were only younger rocks carried into the midst of older beds by dislocations.[3] Barrande's idea was that younger faunas are sometimes intercalated with older ones by changes in physical geography. The modern doctrine of colonies. on the other hand is that older faunas have often been preserved by survival in places where no great changes have taken place, and that these older faunas have been intercalated with the younger by changes in physical geography.

Heterochronous appearance.—By heterochronous appearance of forms is meant their occurrence at different horizons in separated regions. Now it is well known that a species seldom occurs at exactly the same time in two widely separated places; it must originate at the one and migrate towards the other. This migration takes time, and the species may be entirely extinct at the point of origin before it reaches the second place. But geologists have commonly used species as criteria of horizons, when in reality this should be subject to much greater limitations than even the ideas of homotaxis, as formulated by Huxley,[1] would demand.

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[1] Jahrb. K. K. Geol. Reichsanstalt Wien. Bd. 28, 1878. Ueber unvermittelt auftretende Cephalopodentypen im Jura Mittel-Europas.

[2] Système Silur. Centre Bohème, Vol. I., p. 73, etc.

[3] J. E. Marr, Quart. Jour. Geol. Soc., 1880, p. 605, 1882, p. 313.

Faunas need not and do not appear at the same horizon, nor even in the same order of succession, all over the world, for an intermigration between two distant localities would produce an apparent inversion of the two faunas at either place.

The genus *Clymenia*, according to Professor J. M. Clarke,[2] appears in the *Goniatites intumescens* beds of New York ; in Europe *Clymenia* is wholly unknown in the *Intumescens* fauna, but is the characteristic form of the next higher division of the Devonian, where the *Intumescens* fauna is already extinct.

In the Upper Trias, Karnic stage, of California, *Rhabdoceras* and *Halorites* occur, although *Rhabdoceras* is known in the Alps only from the higher Jura stage, and *Halorites* in both Alps and Himalayas is characteristic of the latter horizon. Also in the Hosselkus limestone, Upper Trias, of Shasta county, California, *Trachyceras* and *Protrachyceras* occur, in the zone of *Tropites subbullatus*, and associated in the same rocks with a characteristic *Subbullatus* fauna ; but in the Alps and in the Himalayas *Trachyceras* and *Protrachyceras* are older than the *Subbullatus* fauna, and never occur in the same beds with it. The question then remains, Did *Trachyceras* and *Protrachyceras* survive longer in America than in Asia and Europe, or did the *Subbullatus* fauna reach here earlier? The researches of Mojsisovics[3] show that *Tropites* is probably indigenous to the Arctic-Pacific Triassic province, and that *Trachyceras* is endemic in the Mediterranean region.

Heterochthonous[4] *faunas.*—In many cases faunas appear unheralded by local ancestors, having been brought in by migration from other regions.

Thus in America, according to Professor H. S. Williams,[5] the

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[1] Quart. Jour. Geol. Soc. XVIII., 1862, 46.

[2] Am. Jour. Sci., III. Ser., Vol. XLIII., p. 57.

[3] Arktische Triasfaunen, p. 148 and Abhandl. K. K. Geol. Reichsanstalt Wien., Vol. VI., Part II., Second half, p. 7.

[4] From ἕτερος, *other*, and χθών, *land.*

[5] Cuboides Zone and its Fauna. Bull. Geol. Soc. Am., Vol. I.

Cuboides fauna is exotic, appearing suddenly in the Tully limestone at the base of the Upper Devonian; but in Europe the *Cuboides* fauna belongs to a genetic series, and is autochthonous.

The *Tropites* fauna of the Karnic stage, Upper Trias, is heterochthonous both in Europe, Asia and America, but the place where this fauna belongs to a genetic series is still unknown.

In the same way several of the faunas of the Jura and Cretaceous in California appear to be heterochthonous ; some of these are known to be endemic in certain regions, others, on the contrary, are not.

CONCLUSION.

From the foregoing facts it will be seen that migration increases the struggle for existence by introducing forms into new conditions, to which they must adapt themselves, and that it also breaks up the established equilibrium and introduces new rivals, thus affecting autochthonous forms. Migration therefore works hand in hand with natural selection in killing off weaker forms, and changing the plastic ones by adaptation.

It is also clear that migration strengthens the geologic evidence of great changes in physical geography in past time. Regions that now are continents have certainly been seas, and seas have probably been continents.

Even the ocean abysses need not have been permanent, for their faunas have a modern aspect, and therefore must have changed from the old types. But from what we have seen of survivals of faunas under favorable conditions, we infer that without changes in conditions there is no reason why they should have changed. The natural inference then is that neither continental plateaux nor oceanic abysses have been permanent.

JAMES PERRIN SMITH.

STANFORD UNIVERSITY,
California, May, 1895.